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Research Article

Habitat compression exacerbates human-macaque conflicts: Implications for regional management in karst southwest China

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Abstract

The escalating incidence of human-wildlife conflicts involving protected species has posed a significant challenge in global conservation. Although population growth, a byproduct of successful conservation, has often been pinpointed as a key factor, the impact of human-induced land use changes and habitat loss on conflict occurrence has not been well comprehended, especially at broader regional levels. In China's mountainous southwest, conflicts between humans and the nationally protected rhesus macaque (*Macaca mulatta*) have intensified due to agricultural encroachment into forested zones. This study integrates species distribution data (309 occurrence points) and conflict incident records (252 sites) across a 16,800 km^2 karst landscape to evaluate habitat suitability under natural versus anthropogenic scenarios using the MaxEnt model. Our findings reveal that Precipitation of Wettest Quarter (bio16), Normalized Difference Vegetation Index (NDVI), Mean Diurnal Temperature Range (bio2), Minimum Temperature of the Coldest Month (bio6), and Human Population Density (pop) are the predominant determinants of macaque habitat suitability at a regional scale. There is a substantial spatial correlation between high habitat suitability zones and areas prone to conflict incidents. Moreover, human activities have markedly modified the extent and distribution of macaque habitats. Our results imply that the escalating severity of protected species incidents at a regional scale may not be solely due to population growth but also to human-driven land use changes that increase the spatial overlap between suitable habitats and human activity areas. Consequently, effective management strategies for protected species incidents should place a heightened emphasis on habitat modifications.

Key words: Environmental determinants, habitat suitability, human-wildlife conflicts, land use changes, Rhesus macaque (*Macaca mulatta*)

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Introduction

Human-wildlife conflicts (HWC) have indeed emerged as a significant concern in the realms of biodiversity conservation and management research (Nyhus 2016). There has been a prevalent belief that the primary driver behind the rise in wildlife incidents is the growth in wildlife populations, attributable to

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ecological improvements (Su et al. 2022). Conversely, another perspective has suggested that alterations in wildlife habitats, leading to increased overlap with human-activity zones, are major contributors to these incidents and the escalating conflicts they engender (Marco et al. 2019; Markov et al. 2019). Despite these differing views, there has remained a paucity of empirical research providing robust evidence to substantiate either stance.

The rhesus macaque (*Macaca mulatta*), a Class II protected species in China, exemplifies this conservation dilemma. As the most widespread non-human primate in Asia, its ecological plasticity enables adaptation to fragmented habitats, yet this adaptability also fueled conflicts (Martinez-Abrain et al. 2019). Recent population surges in southwestern China have led to widespread crop-raiding, with 68% of incidents occurring in maize fields adjacent to forest edges (Fang et al. 2024; Li et al. 2024). However, current management strategies have predominantly focused on population control (e.g., sterilization programs), neglecting the potential of habitat-based interventions (Kansky 2022), a critical oversight given that macaque habitat selection in rural agroforestry mosaics, particularly in karst ecosystems, is poorly understood compared to urban populations (Anand et al. 2018; Davoli et al. 2022).

In recent years, incidents involving macaques have been reported in various regions of China, particularly in the mountainous areas of the southwestern region (Li et al. 2024). Our research site, Qianxinan Buyi and Miao Autonomous Prefecture, a 16,800 km^2 karst region in Guizhou Province, offers an ideal model to address these gaps. Characterized by conical karst formations, steep elevation gradients (275–2,196 m), and a mosaic of forests (60.2% coverage) and farmland (18.7%), this region sustains high macaque densities while experiencing severe agricultural losses (Qianxinan Prefecture People's Government 2024). Its unique geomorphology and agroforestry gradients, shaped by long-term ecological network evolution (Deng et al. 2024), support diverse protected species such as Lady Amherst's pheasant (*Chrysolophus amherstiae*) (Bi et al. 2020; Yang et al. 2022). More than 70% of conflict incidents reported between 2021 and 2024 occurred in maize cultivation zones bordering forest patches (Fig. 2c, d), yet the environmental drivers of macaque habitat use in such landscapes remain unquantified. This knowledge gap impedes the design of spatially targeted mitigation measures, as current policies lack evidence-based thresholds for habitat suitability or conflict risk.

To bridge this gap, our study integrates species distribution modeling and conflict incident mapping to address two objectives: firstly, to identify key determinants of macaque habitat suitability at a regional scale, disentangling the relative contributions of natural environmental factors (e.g., precipitation, vegetation) and human activities (e.g., population density, road proximity); secondly, to quantify habitat compression effects by comparing suitability patterns under natural versus anthropogenic scenarios, and evaluate their spatial congruence with conflict hotspots.

By combining MaxEnt modeling with field-validated conflict data, we aim to challenge the prevailing assumption that population growth alone drives HWC escalation. Instead, we propose that habitat compression—mediated through land-use changes—serves as a critical yet understudied mechanism. Our findings will inform spatially explicit management strategies to balance macaque conservation with agricultural livelihoods in karst regions, with broader relevance to human-wildlife coexistence in biodiverse yet socioeconomically vulnerable landscapes.

Study area

The Qianxinan Buyi and Miao Autonomous Prefecture (located between 24°38'–26°11'N, 104°35'–106°32'E) is strategically positioned at the confluence of Yunnan Province, Guizhou Province, and the Guangxi Zhuang Autonomous Region. Spanning an expansive area of 16,800 square kilometers, this region encompasses eight counties and cities. The topography is distinctive, with a gradient that descends from higher elevations in the west to lower elevations in the east. The area is renowned for its low-latitude, high-altitude mountainous terrain, with altitudes varying from 275 to 2,196 meters, and is recognized as a significant exemplar of the world's conical karst geological formations (Fig. 1). The region enjoys favorable hydrological and thermal conditions, being part of the Nanpan River and Beipan River basins within the Pearl River system. The climate is classified as subtropical monsoon humid, with an average annual precipitation of 1,352 mm and temperatures fluctuating between 13 °C and 19 °C (Deng et al. 2024). The prefecture boasts a rich biodiversity, harboring numerous species under protection, including the rhesus macaque, Lady Amherst's pheasant, silver pheasant (*Lophura nycthemera*), leopard cat (*Prionailurus bengalensis*), Guizhou sapsucker (*Cycas guizhouensis*), balsam leaves (*Lindera communis*), spoke flower chicory (*Oreocharis esquirolii*), and forked spore sapsucker (*Cycas segmentifida*) (Bi et al. 2020; Yang et al. 2022).

According to the 2022 data released by the local government, the Qianxinan Prefecture boasts an extensive area of forested land, amounting to 1,010,876 hm^2, which constitutes 60.2% of the total land area. Additionally, the arable land spans 314,434 hm^2, representing 18.71% of the total area, thereby underscoring the region's pronounced agroforestry characteristics (Qianxinan Prefecture People's Government 2024). In recent developments, there has been a marked uptick in incidents involving macaques across the prefecture's counties. Distinct from their counterparts in urban parks, these macaques are purely wild, traverse in groups and exert a significant impact on agricultural produce (Fang et al. 2024).

Methods

Macaque distribution data acquisition

Between April 2021 and July 2024, we conducted a comprehensive data collection program to map the distribution of macaques using a combination of line transect, interviews, and infrared camera monitoring. This approach initially gathered 309 accurate distribution points (Fig. 1) and 252 hazard points (Fig. 7) across forests, shrublands, and human-modified landscapes in both high and low NDVI areas of Qianxinan Prefecture.

The macaque distribution data included direct sightings of individual macaques as well as indirect evidence such as feces, hair, injury signs, and other markers indicating the presence of macaques. The macaque hazard data was developed through a structured questionnaire of 237 households in conflict-prone villages to identify patterns of location and timing of crop damage, followed by field inspections to verify these conflict sites and exclude damage not associated with macaques (e.g., *Sus scrofa*). Crucially, our stratified sampling design ensures that survey effort is equally distributed across high and

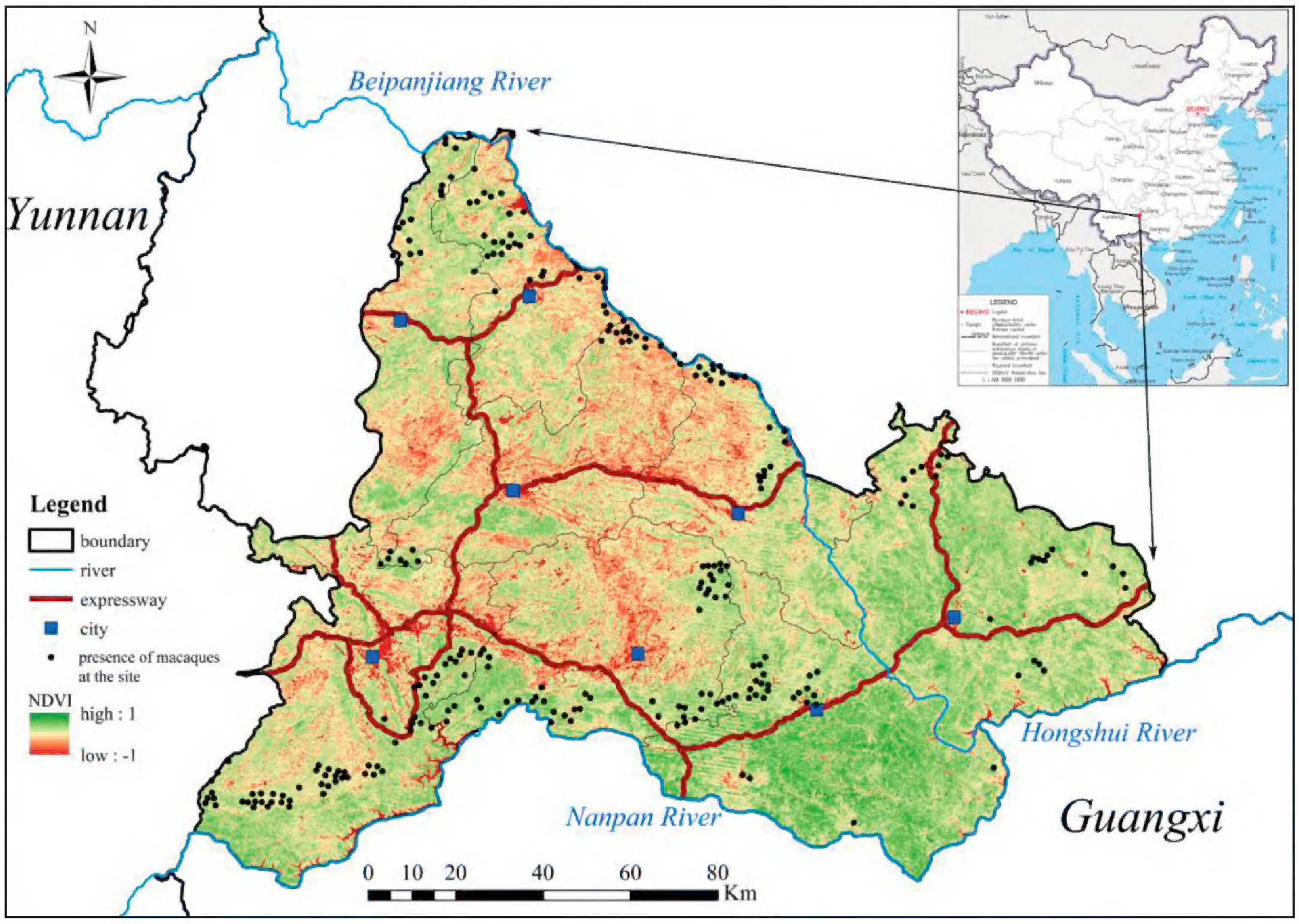

Figure 1. Distribution of macaques in this study site (The presence sites of macaques represent the sites recorded in the actual survey, and the low NDVI region recorded fewer wild macaques).

low NDVI habitats, maintaining standardized protocols to minimize spatial bias. However, no evidence of wild macaque distribution was found in low NDVI areas.

In order to minimize the impact of local spatial clustering and enhance the model's accuracy, we implemented spatial filtering techniques. This involved the removal of data points that were in close proximity, specifically less than 1 kilometer apart. Through this rigorous process, the dataset was refined to 259 final distribution points. These points were subsequently formatted into a CSV file, aligning with the requirements for input into the MaxEnt model (Li et al. 2023).

Environmental variables and multicollinearity reduction

Expanding upon the foundational research into the spatial distribution of non-human primates and the ecological behaviors of macaques (Chen et al. 2019; Yao et al. 2022), this study has identified 26 environmental variables linked to macaque distribution (Table 1).

- Climate: 19 bioclimatic layers (WorldClim v2.1, 30" resolution).
- Topography: Elevation, slope (SRTM 30 m DEM).
- Vegetation: NDVI (MODIS 16-day composite, 250 m).
- Anthropogenic: GDP, population density (WorldPOP 100 m), road/river proximity.

Variables were resampled to 30 m resolution and converted to ASCII format. To address multicollinearity, pairwise Pearson correlations ($|r| \geq 0.8$) were calculated (Fig. 3) the variable with higher ecological relevance was retained. Final predictors included 8 natural (bio2, bio6, bio14, bio16, altitude, slope, NDVI, river distance) and 3 anthropogenic factors (GDP, population, road distance).

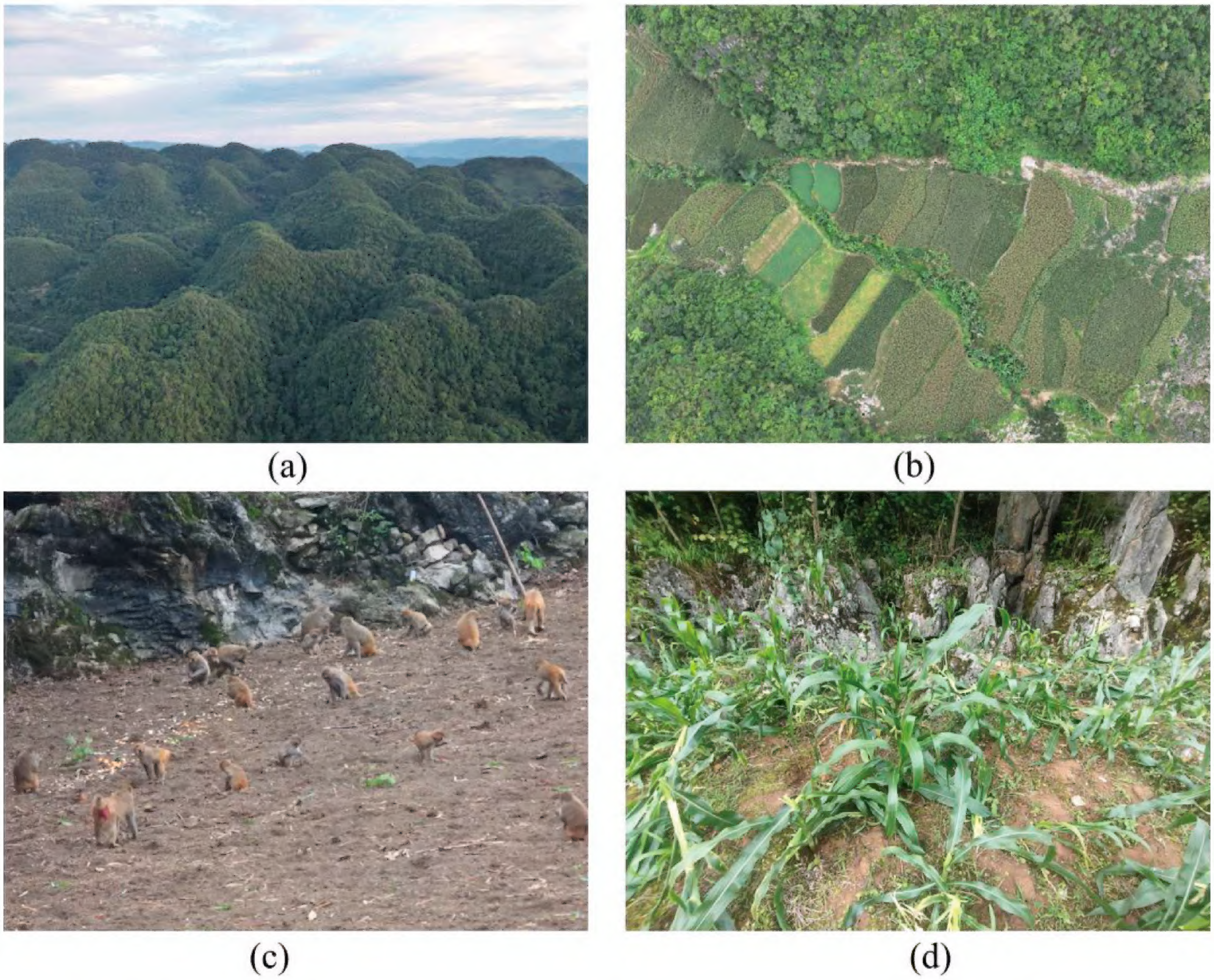

Figure 2. The distribution of forest vegetation, agricultural land status, and crop damage caused by rhesus macaque in Qianxinan Prefecture **a** displays the current distribution and coverage of forest vegetation in Qianxinan Prefecture **b** shows the distribution of maize crop cultivation in the mountainous agricultural areas of Qianxinan Prefecture **c** depicts macaque groups foraging in agricultural land **d** highlights maize crop damage resulting from macaque activity.

Habitat suitability modeling with MaxEnt

The spatially filtered macaque distribution points and environmental variables were then integrated into MaxEnt. The model's optimal parameters were calibrated by allocating 25% of the data for validation and 75% for training, with the remaining settings adhering to the univariate model's parameters. A probability threshold of 0.5 was applied for predictions, and a Jackknife procedure was employed to assess the significance of individual variables. The model's efficacy was gauged using the Area Under the Curve (AUC) of the Receiver Operating Characteristic (ROC) curve, with an AUC score below 0.6 indicating a non-informative model, a score between 0.6 and 0.7 suggesting poor predictive ability, 0.7 to 0.8 indicating average performance, 0.8 to 0.9 signifying good performance, and a score above 0.9 being considered excellent (Sun et al. 2023).

Habitat classification and spatial overlap analysis

To assess the influence of natural environmental factors and human activities on habitat suitability, habitat suitability predictions were generated under two scenarios: one based solely on natural environmental factors and another that included

Table 1. Candidate environmental variables and sources.

Category	Abridge	Variable	Source
natural environment	bio1	Annual mean temperature (°C)	WorldClim (Fick and Hijmans 2017)
	bio2	Mean monthly temperature range (°C)	
	bio3	Isothermal (%)	
	bio4	Temperature seasonality (°C)	
	bio5	Max. temperature of warmest month (°C)	
	bio6	Min. temperature of coldest month (°C)	
	bio7	Temperature annual range (°C)	
	bio8	Mean temperature of wettest quarter (°C)	
	bio9	Mean temperature of driest quarter (°C)	
	bio10	Mean temperature of warmest quarter (°C)	
	bio11	Mean temperature of coldest quarter (°C)	
	bio12	Annual precipitation (mm)	
	bio13	Precipitation of wettest month (mm)	
	bio14	Precipitation of driest month (mm)	
	bio15	Precipitation seasonality (Dimensionless)	
	bio16	Precipitation of wettest quarter (mm)	
	bio17	Precipitation of driest quarter (mm)	
	bio18	Precipitation of warmest quarter (mm)	
	bio19	Precipitation of coldest quarter (mm)	
	Altitude	Altitude (m)	Computer Network Information Center of the Chinese Academy of Sciences (https://www.gscloud.cn)
	Slope	Slope (°)	
	NDVI	Normalized Difference Vegetation Index	Resource and Environmental Science Data Center (https://www.resdc.cn)
	dis_rive	Distance to river (m)	
human activity	GDP	gross domestic product	
	dis-road	Distance to road (m)	
	Pop	population density (number/100 m²)	WorldPOP (https://hub.worldpop.org)

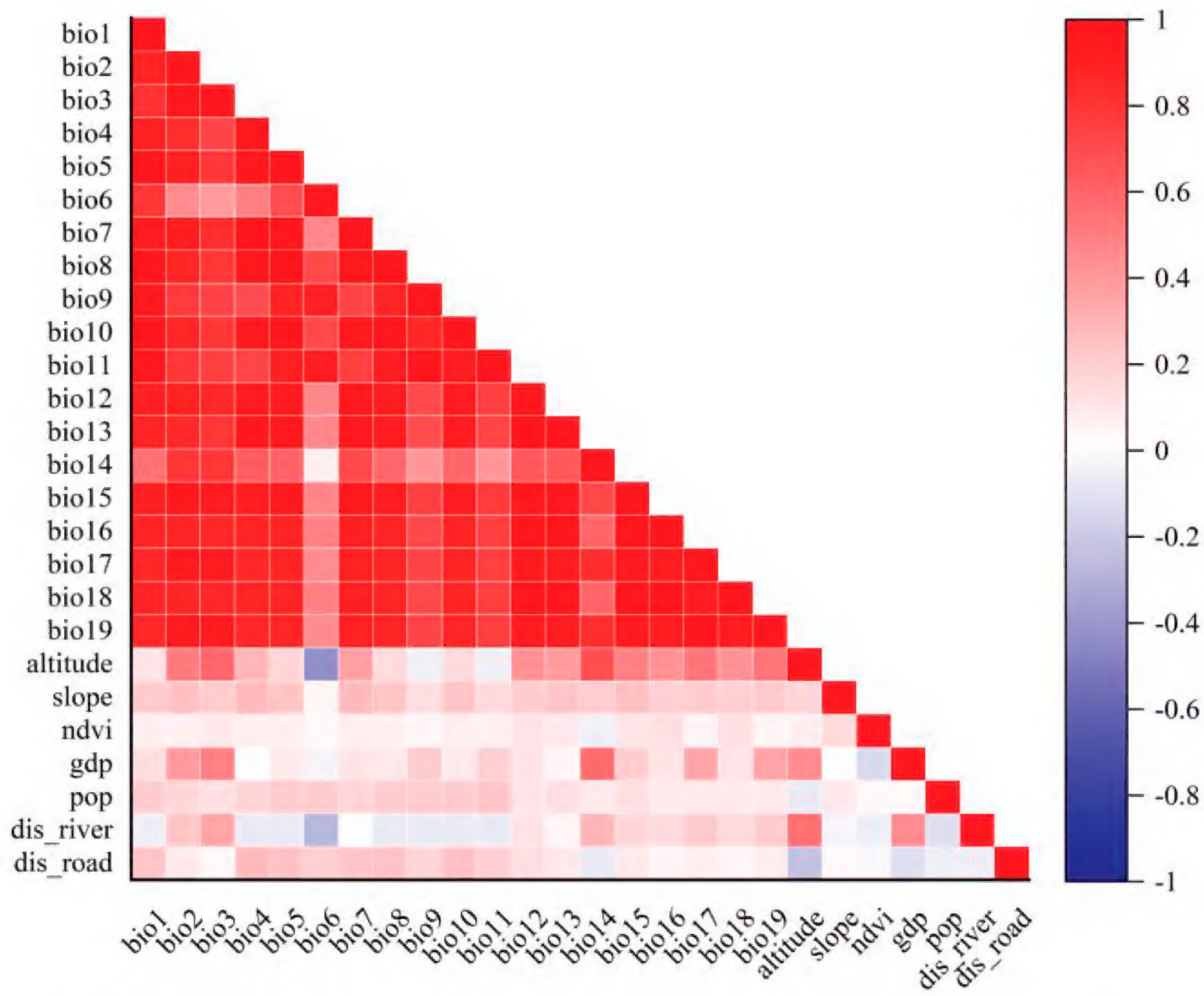

Figure 3. Results of Person correlation test between environmental variables (see Table 1 for environmental variables).

both natural and human factors. The outcomes for each scenario were averaged over 10 iterations to derive the final predictions (Qian et al. 2022; Gu et al. 2023).

Maxent model's output was subsequently imported into ArcGIS 10.7 for reclassification. Employing the natural breakpoints method, macaque habitat suitability was stratified into four classes: highly suitable (>0.75), moderately suitable (0.50–0.75), low suitability (0.25–0.50), and unsuitable (≤0.25) (Yang et al. 2024). Spatial overlap between macaque incident locations and suitable habitat areas under both scenarios was analyzed to evaluate the degree of congruence between incidents and areas of diminished habitat suitability. All data analysis, processing, and visualization were executed using SPSS 26.0, MaxEnt 3.4.4, and ArcMap 10.7.

Results

Model prediction accuracy

The outcomes from the ROC curve analysis revealed that the Area Under the Curve (AUC) was 0.847 (±0.023) when the model was restricted to natural environmental factors alone (Fig. 4a). When both natural environmental and human activity factors were integrated into the model, the AUC value increased to 0.867 (±0.022) (Fig. 4b). These AUC values suggested that the model exhibited robust performance in both scenarios, offering a high degree of accuracy in the prediction of suitable habitats for rhesus macaque within the study area. The marginal increase in the AUC value under the combined factors scenario indicated that the model's predictive power was enhanced when accounting for both natural environmental conditions and human activities. This suggested that anthropogenic factors, including population density and road proximity, significantly influenced the determination of suitable macaque habitats in the region under study.

Effects of environmental factors on macaque population distribution

Under the influence of natural factors alone, the variable that exerted the most significant impact on macaque distribution was bio16, with a contribution of 34.4%, followed closely by NDVI at 23.8%. In contrast, the impact of variables such as distance to river (dis_river, 2.1%), slope (2.1%), altitude (2.0%), and bio14 (1.4%) was negligible. The model identified bio16, NDVI, bio2, and bio6 as the primary contributors, collectively accounting for 90.2% of the total contribution to macaque distribution.

When both natural and human factors were taken into account, the top four contributors shifted slightly, with bio16 retaining its prominence at 29.0%, NDVI at 20.9%, bio2 at 13.5%, and population density emerging as a significant factor at 12.7%. Together, these four variables contributed 72.9% to the model's predictive power (refer to Table 2). This change underscored the substantial influence of human factors, particularly population density, on the distribution of macaques in the study area.

Among the four most influential environmental factors—bio16, NDVI, bio2, and population density (pop)—their impact on the distribution of macaques follows similar trends when examining natural factors (Fig. 5) and when

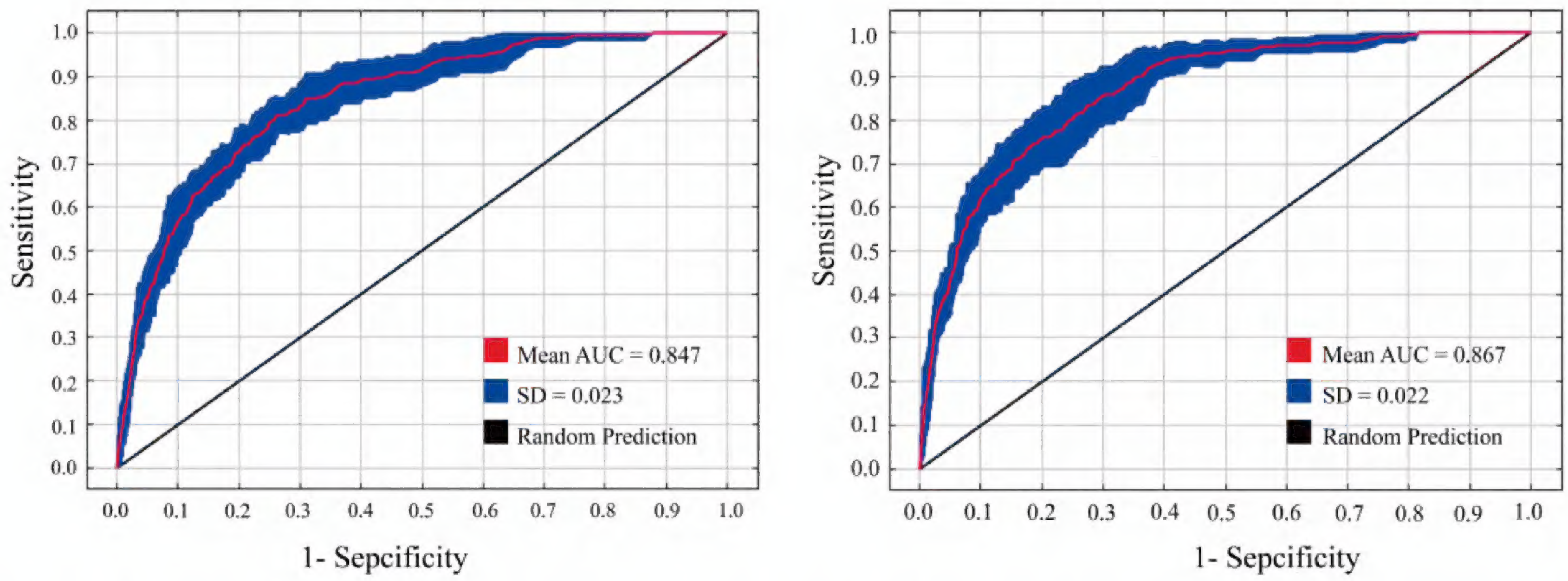

Figure 4. ROC curves for the MaxEnt model predicted the spatial distribution of macaque (**a** natural environment factors **b** combined factors).

Table 2. Environmental variables used in predicting suitable habitats for macaque and their contribution values.

Variables	Percent contribution (%)	
	Natural environmental factor	Comprehensive factor
bio16	34.4	29
NDVI	23.8	20.9
bio2	16.2	13.5
bio6	15.8	9.5
Bio14	1.4	1.3
dis_river	2.1	3.2
slope	2.1	1.0
altitude	2.0	0.5
pop	–	12.7
dis_road	–	6.8
GDP	–	1.6

considering a comprehensive set of factors (Fig. 6). For bio16, the presence of macaques initially diminished with increasing precipitation, then rebounded, and subsequently declined again, with an optimal rainfall range identified between 580 and 640 mm. Regarding bio2, the likelihood of macaque distribution escalated from approximately 0.36 to 0.85 as the temperature rose, before it began to wane, with the most favorable temperature being around 7.8 °C. The response to NDVI was characterized by a unimodal curve, reaching its zenith at an NDVI value of 0.35 and then tapering off as NDVI values increased further. Additionally, the highest probability of macaque distribution was observed when bio6 was approximately 6 °C. However, as human population density (pop) escalated, the likelihood of macaque distribution plummeted sharply from 0.8–0.9 to 0.1–0.2.

Spatial patterns of habitat suitability and conflict risk

The model's predictive analysis delineated that the optimal macaque habitats were predominantly situated in the eastern sector of the Qianxinan Prefecture, with a particular concentration along the Beipan and Nanpan Rivers. The regions identified as highly suitable, based on a comprehensive assessment

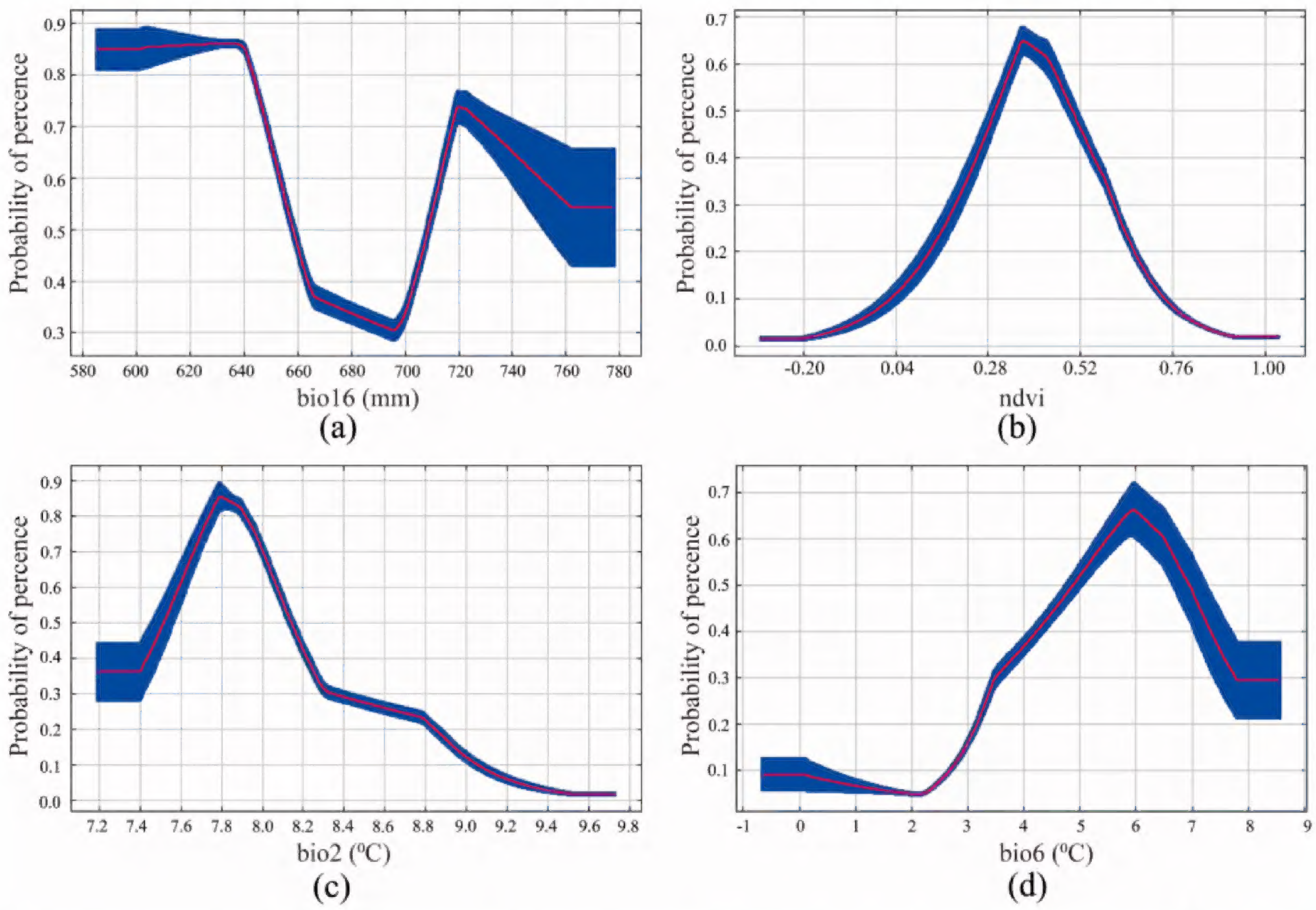

Figure 5. The response curve illustrates the model estimation of macaque distribution probability and the changes in environmental variables influenced by natural factors. The solid line represents the distribution probability of macaques as the variables change, while the blue area indicates the 95% confidence interval. The following trends are depicted **a** the distribution probability of macaques in relation to bio16 **b** the distribution probability of macaques in relation to NDVI **c** the distribution probability of macaques in relation to bio2 **d** the distribution probability of macaques in relation to bio6.

of environmental factors, were predominantly found in Qinglong, Xingyi, and Wangmo counties. These counties collectively constituted 63.36% of the total highly suitable habitat within the prefecture. In contrast, suitable habitats in other areas were characterized by a more fragmented distribution, existing in smaller, dispersed patches.

Under natural conditions, the total area of suitable habitat for macaque was calculated to be 4,987.97 km^2, accounting for 29.69% of the total area studied, which was about 1,093 km^2 larger than the habitat area assessed under comprehensive conditions, indicating that human activities had reduced this area, and it was mainly concentrated in the eastern lowlands with intensive agriculture (Qinglong County and Xingyi County) (Fig. 7b). Overlay analysis of the suitable habitats under natural factors, comprehensive environmental factors, and the locations of macaque-related incidents revealed a clear overlap between the areas where macaque incidents occurred and the regions with reduced suitable habitats (Fig. 7).

Variable importance ranking

Jackknife tests corroborated the dominance of bio16, NDVI, and population density in determining habitat suitability (Fig. 8). Mean diurnal temperature range (bio2) and Minimum temperature of coldest month (bio6) showed secondary importance, while anthropogenic variables (road distance, GDP) exhibited localized effects, particularly in peri-urban zones.

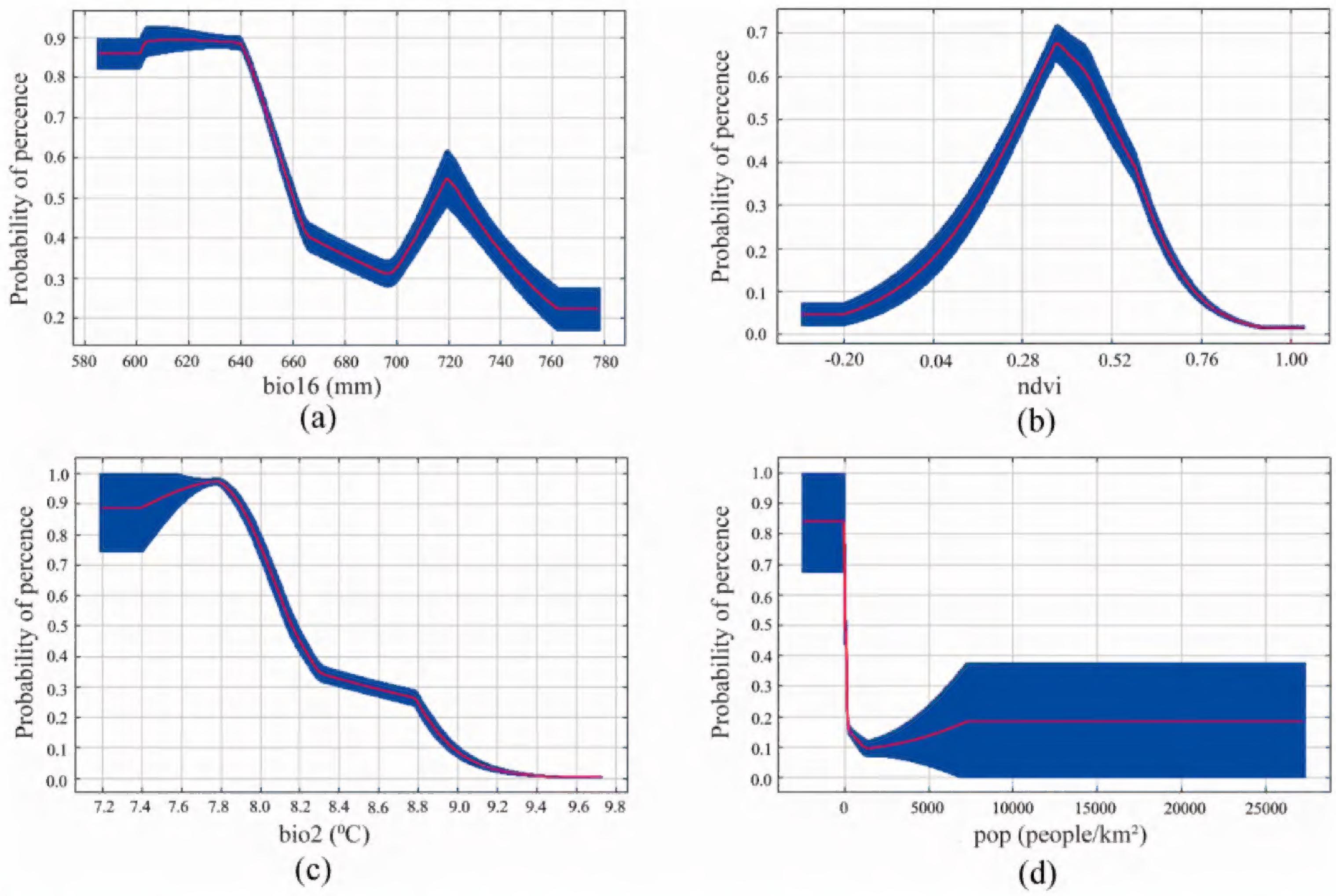

Figure 6. The response curve of the model estimating the probability of macaque distribution and the changes in environmental variables under combined factors. The solid line represents the probability of macaque distribution as the variables change, while the blue area indicates the 95% confidence interval. The subfigures depict the following trends **a** the distribution probability of macaques in relation to bio16 **b** the distribution probability of macaques in relation to NDVI **c** the distribution probability of macaques in relation to bio2 **d** the distribution probability of macaques in relation to population density (pop).

Discussion

Key drivers of macaque habitat suitability

Our study demonstrates that Precipitation of Wettest Quarter (bio16), Normalized Difference Vegetation Index (NDVI), and human population density collectively govern rhesus macaque habitat suitability in karst agroforestry landscapes. The primacy of bio16 (29.0–34.4% contribution) aligns with findings in subtropical primates like Francois' langurs (*Trachypithecus francoisi*), where water availability during monsoons critically influences foraging efficiency and troop mobility (Qin et al. 2024). However, unlike langurs that prioritize vertical cliff refugia, macaques in Qianxinan exhibited stronger reliance on NDVI. This discrepancy likely reflects adaptive foraging in fragmented farm-forest mosaics, where intermediate vegetation cover balances food accessibility and predation risk (Anand et al. 2018; Tian et al. 2019). Such taxon-specific thresholds underscore the necessity of species-tailored conflict management.

Anthropogenic habitat compression and conflict escalation

Habitat suitability has been a pivotal determinant of species distribution and population density, as established by Regolin et al. (2021). It has influenced wildlife interactions within agricultural and forestry landscapes, and has been subject to alteration by climate change and human activities, thereby affecting species distribution and density, as Yang et al. (2024) have noted. These changes have escalated the risk of human-wildlife conflicts at the interface.

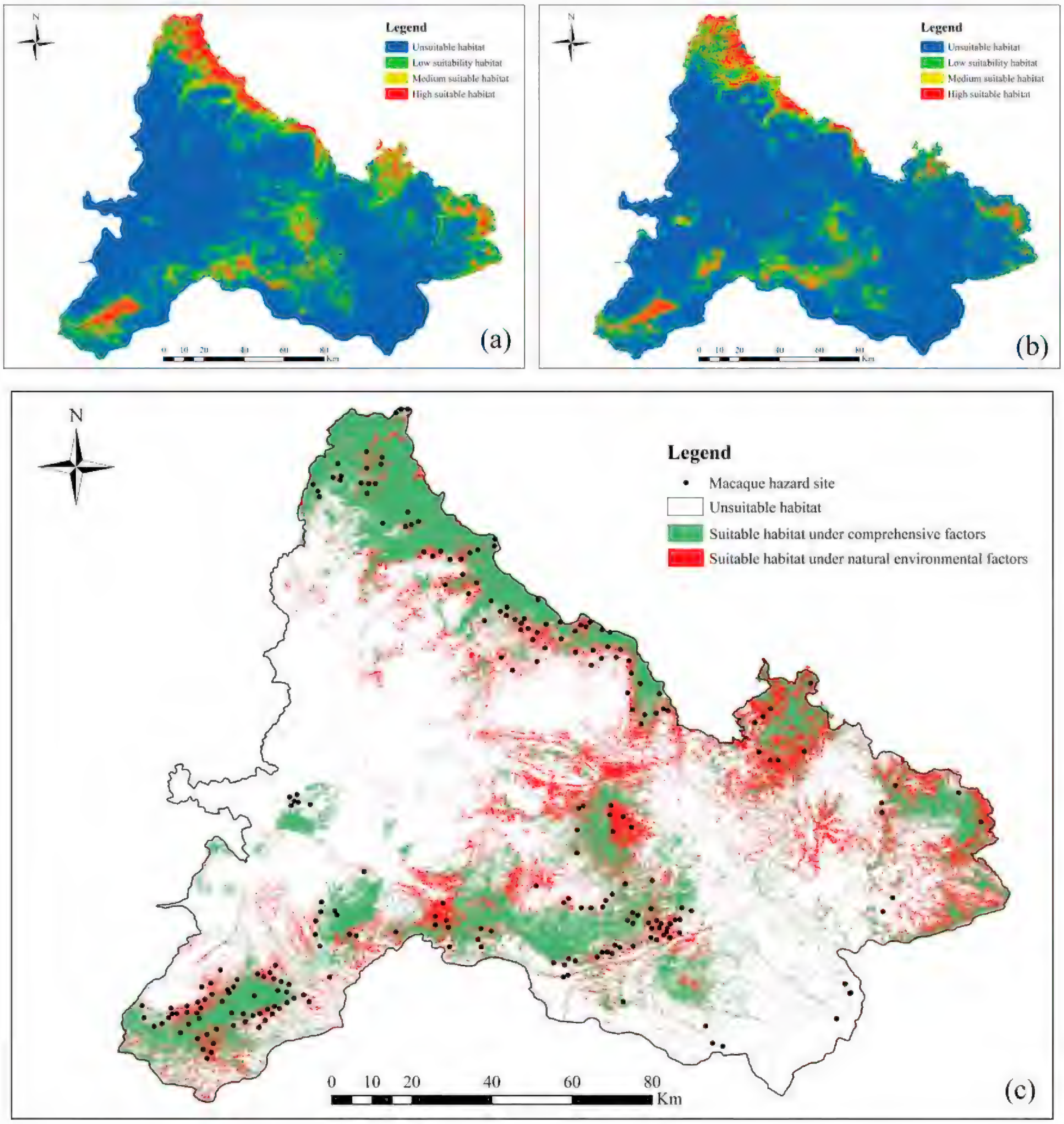

Figure 7. Distribution of Habitat Suitability for macaques **a** suitable habitat for macaques based on natural environmental factors **b** suitable habitat for macaques considering combined factors **c** changes in suitable habitat for macaques under both natural environmental factors and combined factors, along with the locations of hazard events involving macaques.

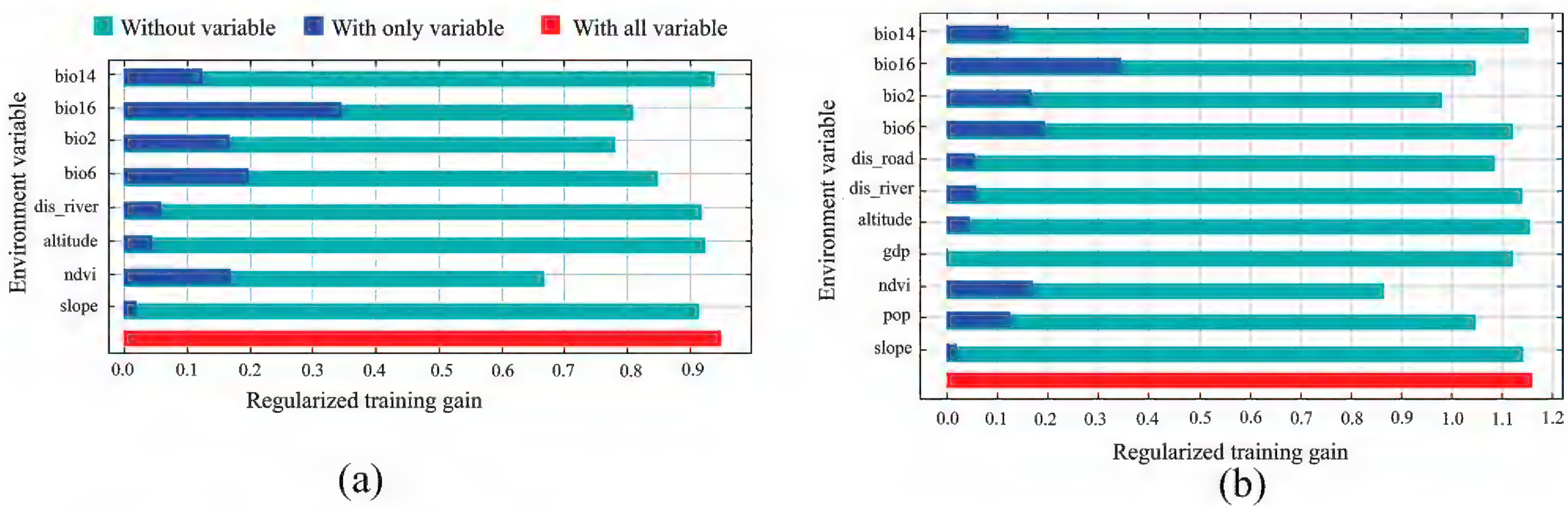

Figure 8. Jackknife test of the significance of key environmental variables on macaque distribution **a** natural environmental factors **b** combined factors.

Our research indicates that human activities have substantially diminished suitable habitats for macaques. This loss of habitat is likely to result in declines in habitat quality, connectivity, and potentially crypticity, as discussed by Pu et al. (2024) and Yin et al. (2024). As noted by Li et al. (2023) and Wang et al. (2024), high population density and GDP growth are linked to habitat loss, fragmentation, and changes in land use, which further contribute to the reduction of macaque habitats. In addition, road construction has intensified habitat isolation and direct disturbances, further shrinking suitable areas, as highlighted by Yang et al. (2024) and Simon F. et al. (2019). The increased frequency of macaque incidents can likely be attributed to shrinking habitats due to escalating human activities, the expansion of human-macaque interfaces, and rapid population growth, as suggested by König et al. (2020) and Tsunoda and Enari (2020). This compression has forced macaques into suboptimal habitats near human settlements, which helps explain the spatial consistency observed between conflict hotspots and habitat edges (Davoli et al. 2022).

Reconciling conservation and agricultural livelihoods

Current macaque management in China predominantly employs population control (e.g., sterilization), yet our findings advocate for habitat-centric strategies. Three actionable measures emerge: Core habitat restoration: Prioritize reforestation in high-suitability zones (Qinglong, Xingyi) to expand natural foraging areas, targeting NDVI enhancement from 0.35 to 0.55 - a threshold associated with 50% reduced crop-raiding in our response curves. Buffer zone delineation: Establish 500–800 m ecological buffers along farm-forest edges, integrating non-palatable cash crops (e.g., tea, medicinal herbs) to deter macaque incursions while maintaining farmer incomes. Land-use zoning: Road construction and urban sprawl should be restricted in areas with suitability > 0.75, as guided by our MaxEnt predictions.

Limitations and future directions

While our models captured key regional drivers, three limitations warrant attention: 1) Time dynamics: Static land-use data may underestimate rapid habitat changes; annual NDVI time-series could refine predictions. 2) Behavioral plasticity: Group size and foraging tactics were unmeasured, potentially masking density-dependent habitat selection. 3) Climate change: Future scenarios (e.g., intensified monsoons) may alter bio16 thresholds, necessitating dynamic modeling.

Conclusion and management implications

Key findings

Our study provides robust empirical evidence that human-induced habitat compression, not merely macaque population growth per se, has been the primary driver of escalating human-macaque conflicts in the karst agroforestry landscapes of Southwest China. Precipitation variability (bio16), vegetation productivity (NDVI), and human population density were the principal

environmental determinants of macaque distribution and habitat suitability at a regional level, underscoring the interplay between ecological gradients and socioeconomic pressures.

Policy-ready management strategies

To mitigate conflicts while ensuring macaque conservation, we propose a three-tiered management framework: 1) Core habitat restoration: Prioritize reforestation in high-suitability zones (Qinglong and Xingyi counties) to elevate NDVI from 0.35 to 0.55, which is the threshold for reducing crop damage. 2) Ecological buffer zones: Establish 500–800 m transitional belts along farm-forest edges, incentivizing farmers to cultivate macaque-deterrent crops (e.g., tea, Lindera communis) through subsidies modeled after China's Grain-for-Green Program. 3) Land-use regulation: Restrict road expansion and urban sprawl in areas with suitability > 0.75, guided by spatially explicit zoning maps derived from our models.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

We state that all authors complied with the ethical guidelines of the study and ensured that the study was conducted in accordance with the regulations of the relevant institutions. All data and results are authentic and reliable without any form of falsification or improper manipulation. The content submitted in this article is original and does not contain any unauthorized plagiarism or republication. All individuals who contributed to this study have been recognized in their contribution section. We confirm that we own the copyright or have obtained the appropriate permission to use the images, graphics and other materials in this article.

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Author contributions

Zhicheng ZHANG and Manfang HE: Data curation (equal); formal analysis (equal); investigation (equal); methodology (equal); software (equal); writing–original draft (lead). Ye LI and Haijun SU: Conceptualization (equal); methodology (equal); writing– review and editing (lead).

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Data availability

Data will be made available on request.

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